

THE MECHANISM OF MOVEMENT AND TRANSMISSION OF IMPULSES IN MIMOSA AND OTHER "SENSITIVE" PLANTS: A REVIEW WITH SOME ADDITIONAL EXPERIMENTS.

D. T. MACDOUGAL.

(WITH PLATE XIII)

THE history of investigation of the transmission of impulses in "sensitive" plants begins with the work of Lindsay on *Mimosa* in Jamaica in 1790, which for some reason was not published until 1827.¹ During the century following the subject received no attention except that given it in the north temperate zone, in warm houses, and for the greater part under highly artificial conditions. In such manner it has been the object of numerous series of experiments, and of many highly ingenious speculations.

Briefly summarized, the aggregate results of both methods embrace nothing beyond a delineation of the anatomical details, the chemical properties of some of the tissue systems, an immense number of the features of reaction under artificial conditions, "working theories" of the mechanism of the motor organs and metaphysical explanations of the transmission of impulses, and general relation of such highly specialized forms of sensitiveness to the developmental history of the plant.

The work upon the subject under conditions necessarily artificial has been so futile in real results that it has come to be admitted on all hands that a satisfactory solution of the problems presented may be accomplished only by researches prosecuted in the tropics, in the habitat of plants which have acquired a high degree of sensitiveness.

¹Quart. Jour. Sci. Lit. and Art 24: 79. 1827, and 25: 434. 1828.
1896]

As an account of such an attempt the recent work of Cunningham deserves attention.²

As a basis for the theory upon which this author seeks an explanation of the mechanism of pulvini he devotes a large proportion of his work to the demonstration of the novel idea "that the great majority, if not all, of the transient spontaneous movements of higher vegetable organisms, whether of a nyctitropic character or arising in connection with other conditions than the incidence or removal of sunlight, are not dependent upon the presence of any specially irritable and contractile protoplasts within the motor organs, but on purely physical processes connected either with fluctuations in the osmotic capacities of the tissue-elements, or with alterations in the relations existing between local and general supply and loss of water." In support of this remarkable statement, but very little evidence obtained by an examination of the cell is advanced, but dependence is placed upon the external consistency and color of organs subjected to various reagents. Thus flowers of Hibiscus with the peduncle in water were exposed to ammonia gas in a moist chamber, and as they did not lose their form, while flowers similarly exposed to chloroform wilted, the conclusion was drawn that the osmotic activity of the dead cells was increased by the ammonia in the first instance. A final conclusion derived from similar experiments was that "there is no direct relation between turgidity and the presence of living protoplasm in the turgid elements," but in some instances turgidity may be indirectly dependent on the protoplasm because of the necessity for the manufacture of osmotically active substances; a conclusion certainly at variance with almost all of the known facts concerning the physiology of the cell. Not only does the author deny the possibility of changes in the filtrative properties of protoplasm, but he disregards the simple physical properties of this colloidal substance. He proposes a design

²CUNNINGHAM, D. D.: The causes in the fluctuations in the motor organs of leaves. *Annals of the Bot. Gard., Calcutta* 6: 1-145. 1895. 4to. 7 lith. col. plates.

for the construction of a machine which shall react similarly to *Mimosa*.

All pulvinar movements are supposed to be due to a loss of water from the portion of the pulvinus in which contraction ensues, either directly by transpiration, or by withdrawal by the action of neighboring tissue so affected.

Scant attention is paid to the results of Pfeffer and his students, but the author gives the records of a very large number of experiments which, as he rightly points out, show reactions quite different from those obtained in northern latitudes. The thermometric records are meager in certain series, but it is possible that the temperature variations do not exert such an important influence in the tropical habitat of the plant.

According to Haberlandt³ and others, the transmission of impulses and reaction in *Mimosa* bears a direct relation to the conditions securing an excessive root supply of water and hindered transpiration. Cunningham, however, finds the relation an inverse one, that plants in a saturated atmosphere react least readily. In a comparison of the three most important forms of stimuli he says: "In cases of 'contact stimulation' we induce mere local distributions of liquid within the tissues; in cases of incision we give rise to temporary exudations from the general supply of liquid; in cases of heating we secure not only this, but in addition we establish temporary increase of transpiratory loss and a site of persistent abnormal drain." In what manner a contact stimulus may cause alterations in the transpiration of a cell without the interposition of protoplasmic action is not explained. It must be said, however, that Dr. Cunningham's observational results are of great value, and are very suggestive as to methods useful in a continuance of the work.

ADDITIONAL EXPERIMENTS.

During the summer of 1895 I was enabled to make a number of experiments with a view of determining the chief factors

³ Reizleitende Gewebesystem der Sinnpflanze. 1890.

in the transmission of impulses by *Mimosa* and other plants, in the Botanical Institute at Leipsic by the courtesy of Geh. Professor Pfeffer, to whom I am also indebted for his untiring attention and advice.

A number of the tests were repeated in the Botanic Institute at Tübingen in the present year, and I am indebted to the director, Professor Vöchting, for the opportunity. Some of the tests have also been repeated in the plant houses of the University of Minnesota.

Haberlandt's conclusions as to the transmission of impulses by means of hydrostatic disturbances in a series of elongated cells (the "Schlauchzelle") lying externally to the xylem have been received with general favor, and accounts for such a large number of the phenomena of transmission that certain of the experiments were arranged in such manner as to test the capacity of this theory for final explanation.

In the first place, repetitions were made of the well known experiments in which impulses were transmitted through portions of stems and petioles which had been killed by steam or dry heat in such manner as to allow the dead portions to remain mechanically intact. In my own work this was accomplished by winding soft cloth around the portion to be killed and saturation with water at 90–100° C. for five minutes. In some instances the dead portions were allowed to desiccate and in others a wrapping of tinfoil or a sheath of oiled plaster of Paris prevented undue loss of moisture.

I was able to transmit impulses from an incision or flame through dead portions of stems 3^{cm} in length; in some instances in which desiccation had proceeded to such an extent that the cell lumina of the dead portion were quite devoid of liquid contents, and in one instance through a portion bent at right angles by the weight of the leaf.

I was able to obtain similar transmissions in the midrib of the multipinnate leaf of *Oxalis sensitiva*, which offers many of the features of *Mimosa*.

In a few instances a reaction was obtained when incisions

were made in the dead portion of a stem or petiole of *Mimosa*, but no great reliance is placed in such results.

Dr. Cunningham has repeated the tests of transmission through dead portions of stems, and was able to send an impulse through stems consisting of alternating living and dead sections.

The above experiments, giving similar results in the hands of a great number of workers, demonstrate conclusively that transmission may be accomplished in portions of the plant in which no turgid cells occur, and consequently in which no hydrostatic disturbance is possible.

With such facts in evidence the next step was naturally the determination of the question as to whether or not a hydrostatic disturbance constituted an impulse. Three methods were used. A number of young, healthy plants 40^{cm} in height were brought into the experiment room, and after being cut off near the surface of the soil, the bases of the excised stems were set in beakers of distilled water. The immersed portion (10^{cm} long) of the stem was split and stripped in such manner that a large surface composed of active cells was exposed. When the leaves had regained their normal position half an hour later, with the air temperature at 28–30° C., the water in the beaker was withdrawn and quickly replaced by a saturated solution of potassium nitrate without mechanical disturbance to the shoot. Although the endosmotic action of the potassium must have resulted in the almost instantaneous withdrawal of a large quantity of water from the "Schlauchzelle" and other exposed tissues of the base of the stem, no reaction followed. The leaves were found to be in their usual sensitive condition after the experiment, when contact or incision stimuli were applied.

The bases of the stems of small plants were sealed securely into a glass tube 10^{cm} long, 1^{cm} internal diameter, filled with water, which connected at the other end with a leaden tube 30^{cm} long leading into a receiver of a capacity of 4 liters, with a vacuum of 70^{cm} of mercury. When the leaves had regained their normal position, with the temperature at 28–32° C., the stopcock leading into the vacuum was turned, allowing the full

force of the vacuum to act on the base of the stem. In no instance was a reaction obtained. The usual tests showed a normal degree of sensitiveness in the plant.

The two experiments above described must lead one to conclude that diminished hydrostatic pressure does not constitute an impulse. It is, of course, open to belief that greater variations in pressure or a more sudden application of the same might be followed by a reaction.

To avoid a misconception of the effects of such diminution of pressure on the cell contents, attention is called to the fact that the "Schlauchzelle" form a series of continuous tubes, the contents of which freely communicate by openings in the cell walls, and that variations in pressure on any part of the system are quickly distributed through the entire system, as is demonstrated by the following experiment.

In order to test the effect of increased pressure on the plant, shoots were securely sealed into a short section of glass tubing, as above, by means of a rubber stopper bound in place by wires. The tube was filled with water and the other end connected in a similar manner with a leaden tube, with an internal diameter of 3-4^{mm} and 1.5^m in length, leading to the chamber of a compression air-pump (see plate). When the leaves had regained a normal position in an air temperature of 26-32° C., by a sudden stroke of the handle of the pump a pressure of 3-8 atmospheres was suddenly exerted on the base of the stem, but no reaction followed. That the increased pressure was exerted throughout the plant was proven by the manner in which water poured from the clipped end of a distant leaflet, and that it passed through the "Schlauchzelle" was shown by stripping away the tissues external to these cells. The pressure was thus communicated to distant parts of the plant within a second from the time of its application.

As another test, with its object similar to the above, a compressive pressure was quickly applied to various parts of the plant by the fingers, forceps, or other appliances. In some instances reactions were obtained. It is extremely difficult to

compress the stem quickly without communicating a mechanical disturbance to the plant. It is also difficult to give the compression without crushing the tissues of the plant. It seemed, however, that in the instances where the above faults were avoided no reaction followed the compression, though no conclusions are based on this result.

In conclusion it may be said that the following points are somewhat firmly established: (1) Impulses may be transmitted by *Mimosa* and *Oxalis* through dead portions of stems and petioles in which the conditions are such that a transmission by the cell-wall or the water in the wall only is possible. (2) Great variations in the pressure exerted on portions of the plant in such manner as to set up hydrostatic disturbances extending throughout the entire plant are not followed by reactions; hydrostatic disturbance therefore does not constitute an impulse.

It is to be noted, however, that while it is proven that an impulse may be transmitted by a wall of a dead cell, it does not follow that the entire transmission from the point of reception to the motor organ is accomplished by such means alone. It seems quite possible that protoplasmic action plays a part at both ends of the chain connecting the two points, and that while a hydrostatic disturbance does not constitute an impulse, it may play a minor part in its transmission.

The entire problem, together with that of the developmental history of such highly specialized forms of "sensitiveness" as those exhibited by *Mimosa*, must be followed to their solution in the tropical habitats of the plants.

THE STATE UNIVERSITY OF MINNESOTA.

EXPLANATION OF PLATE XIII.

FIG. 1. Showing branch of *Mimosa* attached to compression pump. A downward stroke of the piston has been given, resulting in the sudden increase of pressure on the base of the excised branch with no reaction of the leaves in consequence. The leaves were then stimulated by a stroke from a pencil, resulting in a normal reaction. The leaden tube in which the

plant is fixed connects with the cylinder at 5 in *fig. 2*. Drawn from a photograph. One-sixteenth natural size.

FIG. 2. Section of compression pump. 1. Fitting around piston rod. The piston rod is driven by the lever handle to which it is connected above. 2. Stopcock leading into the open air; not closed when the pump is used for compression. 3. Piston head moving "air tight" in a metal cylinder. 4. Valve. 5. Outflow pipe through which compressed air is forced. This pipe is extended horizontally in the opposite direction and upward to a point near the base of the crooked lead tube leading to the plant, in the apparatus shown in *fig. 1*. At a point near the juncture with the lead tube it is furnished with a stopcock leading into the open air, which is to be closed during the compression stroke and opened when the stroke is reversed. In *fig. 1* the cylinder is surrounded by a safety casing not shown in *fig. 2*. One-eighth natural size.

The plate for *fig. 2* was copied from the original drawing of the apparatus, and was kindly furnished me by the designer, Mr. Eugene Albrecht, Universitäts-mechaniker, Tübingen, and I am indebted to him for permission to reproduce it here.